

FOSSIL *NEVIUSIA* LEAVES (ROSACEAE: KERRIEAE)  
FROM THE LOWER-MIDDLE EOCENE OF  
SOUTHERN BRITISH COLUMBIA

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ABSTRACT. Fossil leaves assigned to the disjunct rosaceous genus *Neviusia* A. Gray, *N. dunthornei* DeVore, Moore, Pigg & Wehr *sp. nov.* (Rosaceae, tribe Kerrieae) are described from the lower-middle Eocene One Mile Creek locality near the town of Princeton, southern British Columbia, Canada. The leaves are elliptic to broadly ovate, seven-lobed, up to 4.9 cm long  $\times$  5.6 cm wide with craspedodromous venation and two to three sizes of marginal teeth. They bear a striking resemblance to *N. cliftonii* Shevock, Ertter & Taylor, the recently discovered species of the Mount Shasta area of northern California, and differ markedly from the type species *N. alabamensis* A. Gray of southeastern North America. The occurrence in the Okanogan Highlands of *N. dunthornei* marks the first fossil evidence for the small, rosaceous tribe Kerrieae, and further documents the lower-middle Eocene as a time of major radiation of many temperate families, including the Rosaceae.

Key Words: biogeography, Eocene, fossil leaf, Kerrieae, *Neviusia*, Rosaceae

*Neviusia* A. Gray (Rosaceae, tribe Kerrieae; Snow Wreath) is a small genus of flowering shrubs consisting of two extant species, *N. alabamensis* A. Gray of southeastern North America and *N. cliftonii* Shevock, Ertter & Taylor, from the Mount Shasta area of northern California. *Neviusia alabamensis* was first described from Tuscaloosa County, Alabama by Asa Gray in 1859 (Gray 1859; Small 1972). Features of this genus include shrubs with numerous apetalous flowers that bear

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†Wes Wehr died of a heart attack on April 12, 2004.

five white, toothed sepals that extend beyond a flattened hypanthium. The flowers have numerous stamens with conspicuous white filaments and 2–4 pubescent carpels, each with a single pedulous ovule, that mature into drupe-like achenes (Small 1972). The type species, *N. alabamensis*, occurs in the southeastern United States and prefers limestone to shaley cliffs. It is known in a variety of such sites today roughly corresponding with the Mississippi Embayment (Coile 1988; Horn and Somers 1981; Long 1989; Moore 1954).

*Neviusia* has been placed in the small tribe Kerrieae along with the Asian genera *Kerria* DC. (Japanese Rose) and *Rhodotypos* Siebold & Zucc. (Jet Bead; Ertter and Shevock 1993). Features of the Kerrieae include persistent sepals that are either serrate or imbricate and 1–8 drupe-like achenes (Baillon 1869). The tribe was traditionally considered to be intermediate between Spiraeoideae and Rosoideae, two of the traditional four subfamilies of Rosaceae, on the basis of morphological features (Robertson 1974). In contrast to this classification, recent molecular phylogenies support the recognition of two major clades within the Rosaceae that include part of the family (Rosoideae *sensu stricto* and Maloideae *sensu lato*) plus several smaller groups, many at the tribal level, including the tribe Kerrieae. In phylogenetic analyses, relationships among these groups are not well resolved (Judd et al. 2002; Morgan et al. 1994). The tribe Kerrieae nevertheless is always represented as a distinct clade in these analyses and all recognized members of the tribe consistently form a monophyletic clade within large analyses of Rosaceae.

For some time this unusual tribe was noted as an example of the southeastern North American/Asian disjunct distribution recognized for many other angiosperm genera such as *Magnolia*, *Liquidambar*, and *Hamamelis* (e.g., Graham 1999; Li 1952, 1972; Tiffney 1985; Wen 1998). In 1992, a second species of *Neviusia* was discovered, surprisingly, in a remote area of the Mount Shasta region of northern California (Taylor 1993). This second species, *N. cliftonii* (Shasta Snow Wreath), is distinct from the type species *N. alabamensis* in both floral and vegetative characters (Faber 1997; Shevock et al. 1992). In contrast to the apetalous *N. alabamensis*, *N. cliftonii* has white oblanceolate petals, about half as many stamens (50 compared to around 100), shorter sepals and styles, and leaves that are more ovate to cordiform with coarser teeth. Like its southeastern counterpart, Shasta Snow Wreath also grows on limestone substrate, preferring cool canyons near creeks (Shevock et al. 1992).

The occurrence of *Neviusia* at Mount Shasta, California is initially perplexing. However, whereas many closely related disjunct taxa occur

today in the Tertiary refugia of eastern North America and eastern Asia, a number of plants with disjunct distributions can also be cited for northern California and Asia Minor. Examples include such genera as *Dirca* L. (Thymelaeaceae; Leatherwood), and *Calycanthus* L. (Calycanthaceae; Spicebush; Ertter 1993). During the time of the discovery of *N. cliftonii*, fossil floras of the Okanogan Highlands were beginning to provide considerable new information about the diverse lower-middle Eocene vegetation of the Pacific Northwest (Crane and Stockey 1987; Wolfe and Wehr 1987, 1988). These temperate floras, particularly in the localities near Princeton, British Columbia and Republic, Washington, may document the first major radiation of a number of temperate families including the Rosaceae (Wehr and Hopkins 1994), Betulaceae (Crane 1989; Crane and Stockey 1987; Pigg et al. 2003), and the *Acer*-like members of the Sapindaceae (Judd et al. 2002; Wolfe and Tanai 1987).

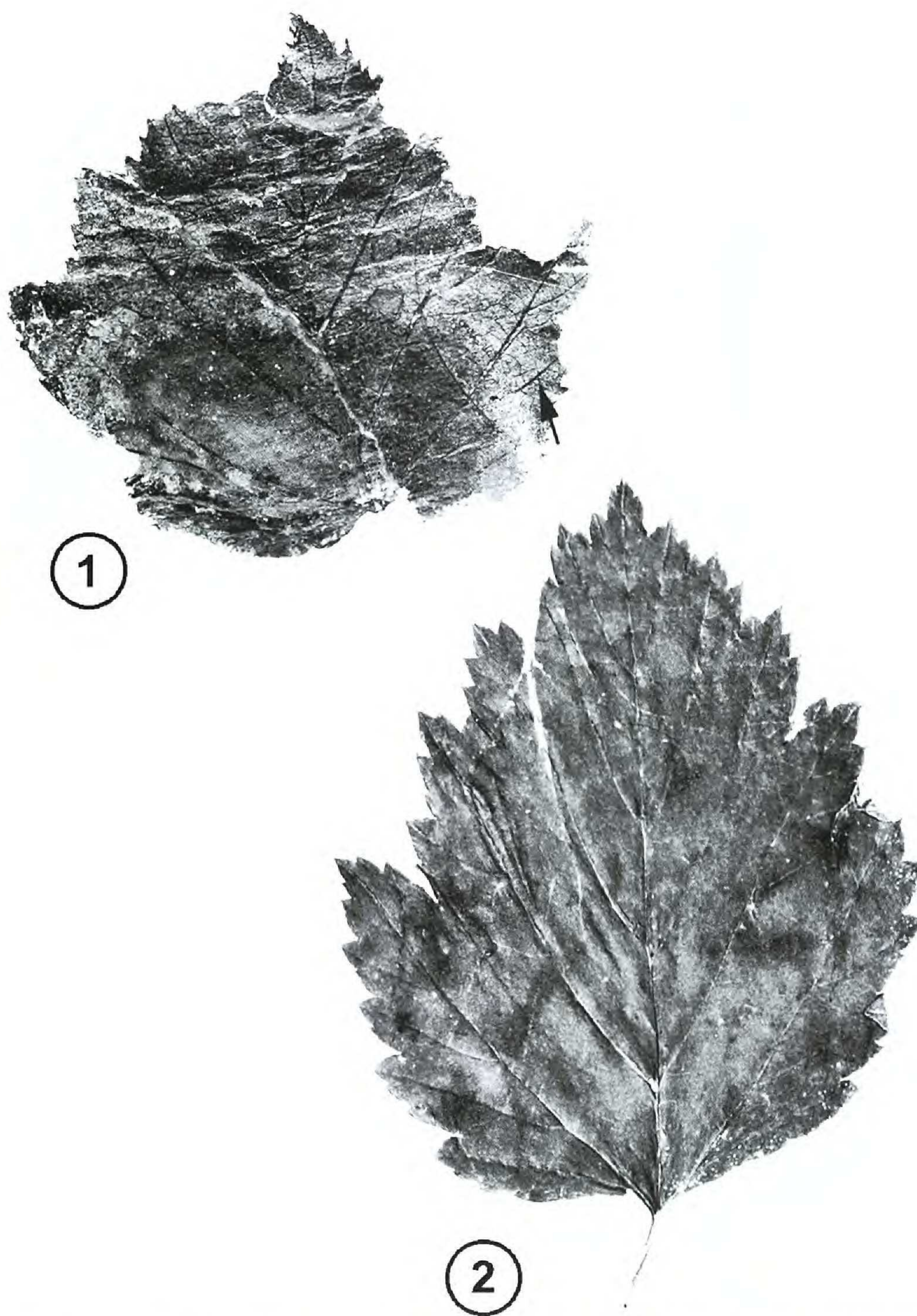
Fossil rosaceous leaves recognized from the Okanogan Highlands floras include both rare and commonly occurring representatives of extant genera from all four traditional subfamilies, as well as several extinct rosaceous forms. Among the genera represented are the rare examples of *Malus/Pyrus*, *Rubus*, and *Amelanchier*, the more commonly occurring *Prunus*, *Spiraea*, and *Crataegus*, and the extinct *Stonebergia* (Moore et al. 2002; Wehr and Hopkins 1994; Wolfe and Wehr 1987, 1988; W. Wehr, unpubl. data). Several specimens that were morphologically similar to the genus *Neviusia* were recognized at the One Mile Creek locality near Princeton, British Columbia and in the Republic flora of eastern Washington state (Wehr 1994; Wehr and Hopkins 1994). Of these, two specimens from One Mile Creek can now be assigned with confidence to *Neviusia*, while the others from Republic lacked diagnostic features and, although rosaceous, are of uncertain affinity. These fossil *Neviusia* leaves have been discussed by several authors (Ertter 1993; Shevock 1993; Stebbins 1993) and are occasionally mentioned in regional floras in connection with living *Neviusia* from California (sometimes inaccurately; e.g., Stuart and Sawyer 2001), but they have never been formally described. In the present contribution we establish the species *N. dunthornei* DeVore, Moore, Pigg & Wehr *sp. nov.* from One Mile Creek, near Princeton, British Columbia, Canada and document its relationship to the two known extant species of *Neviusia*. This fossil occurrence demonstrates the presence of fossil Kerrieae in western North America during the lower-middle Eocene, and figures significantly in our understanding of the phytogeography and early evolution of the rose family during its major Paleogene diversification.

## MATERIALS AND METHODS

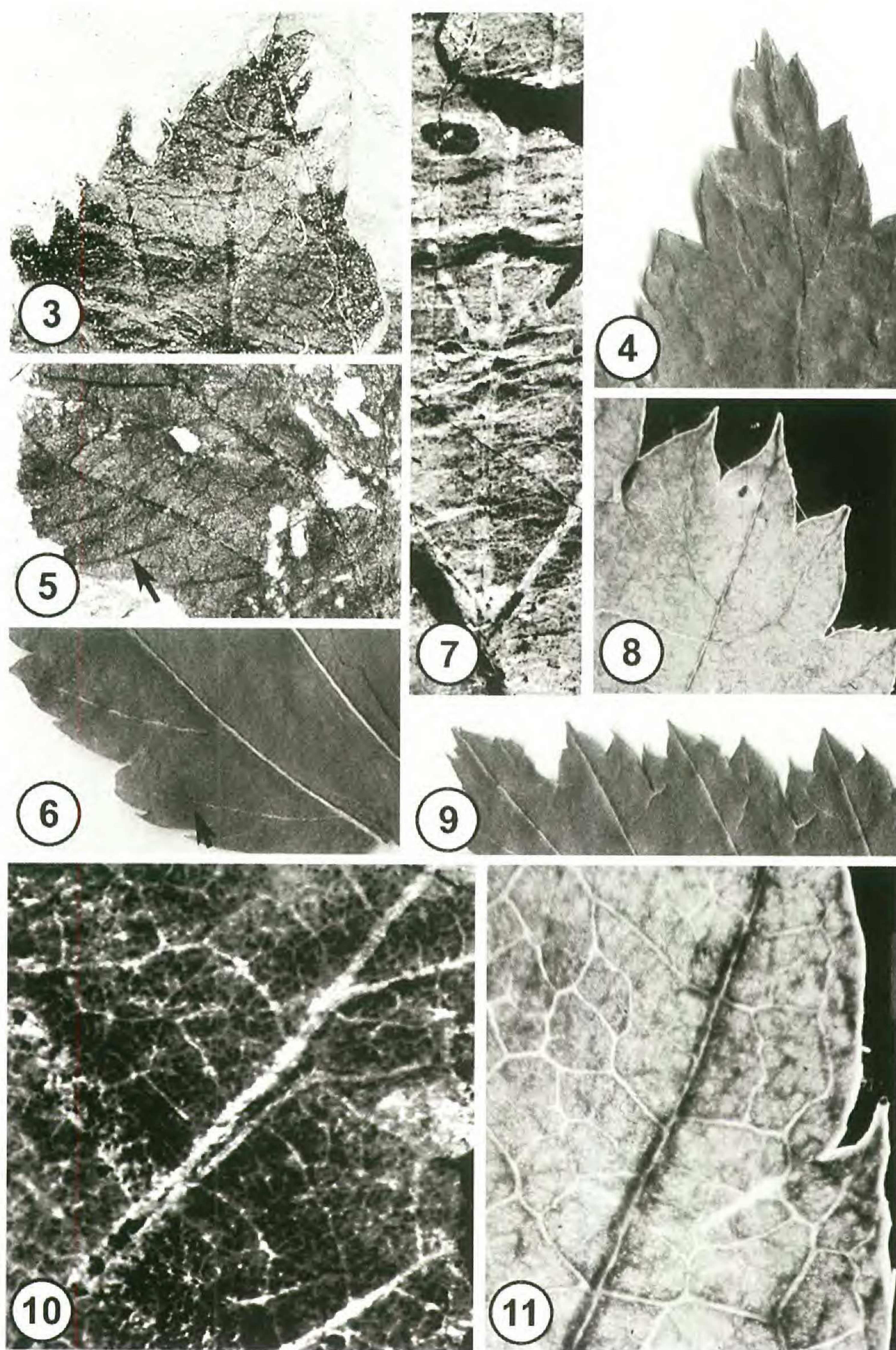
Specimens were collected from the One Mile Creek locality (also known as Allison Creek), in the lower-middle Eocene Allenby Formation, southern British Columbia (Crane and Stockey 1987) in 1991. The locality is 8 km north of Princeton, on the Princeton-Merritt Highway 5, approximately at the confluence of One Mile Creek and Summers Creek (universal transverse Mercator grid: UN 226940). Fossils are preserved as compressions in a finely laminated light green-gray shale that has been interpreted as a lacustrine deposit. Important components of the flora include *Betula leopoldae* (Crane and Stockey 1987), *Acer*, *Aesculus*, *Cercidiphyllum*, *Fagus*, *Prunus*, and rarer *Abies*, pine, and fern remains, although the flora is considerably more diverse than first apparent (Wehr, unpubl. data). Fossil and extant comparative material was photographed and scanned digitally for illustrations. Terminology follows that of the Leaf Architecture Working Group (1999).

## RESULTS

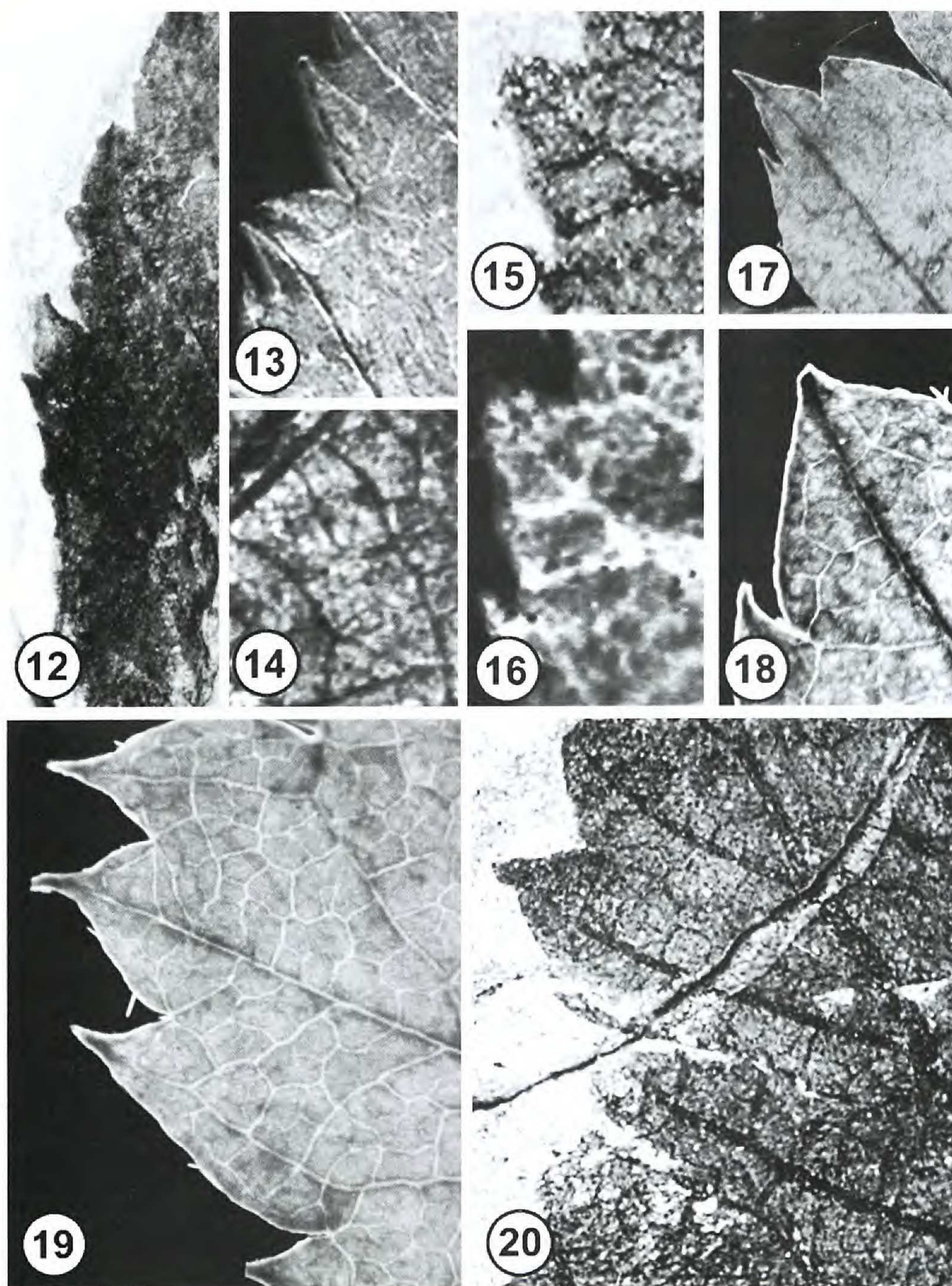
The description of *Neviusia dunthornei* is based on two specimens of leaf compressions. These specimens show details of leaf shape, margin, tooth morphology and several well-preserved orders of venation that can be compared favorably with extant *Neviusia* leaves, particularly those of *N. cliftonii* (Figures 1–20). In one specimen the leaf lamina is slightly folded basally but otherwise complete (Figures 1, 3, 7, 10). The second specimen is more fragmentary but bears excellently preserved detail of venation and leaf margin, and a partially preserved petiole (Figures 5, 12, 14–16). Leaves are up to 4.9 cm long and 5.6 cm wide (length/width ratio 0.88:1), elliptical to broadly ovate, and have up to seven palmately arranged lobes (Figure 1). The leaf apex is slightly acute at an angle of 88°, curves slightly, and is 1.4 cm long (Figures 1, 3), while the lateral lobes are up to 0.7 cm long. One specimen has a petiole that is preserved for 0.8 cm of its length that is up to 2.5 mm wide. While the leaf bases of both specimens are incompletely preserved they are estimated to have an obtuse angle of around 130°. The midrib is thick, up to 1 mm wide, and somewhat curved throughout its course, although this may be in part related to leaf preservation (Figures 1, 7). Secondary venation is craspedodromous with up to seven pairs of relatively broad, suboppositely attached, secondary veins extending from the midrib at an angle of around 30° in the lobes in upper 2/3 of the leaf (Figures 1, 3, 20).



Figures 1–2. Fossil *Neviusia dunthornei* *sp. nov.* and extant *N. cliftonii* leaves, natural size. 1. *N. dunthornei*, holotype specimen (UWBM 54169). 2. *N. cliftonii*.



Figures 3–11. Details of leaf morphology and venation. Figures 3, 5, 7, and 10 are of the fossil leaf, *Neviusia dunthornei*; Figures 4, 6, 8, 9, and 11 are of the extant species, *N. cliftonii*. Figs. 3 & 4. Leaf apex,  $\times 3.5$ . Figs. 5 & 6. Basal leaf area, showing compound agrophic veins (at arrow),  $\times 2.1$ . Fig. 7. Midvein showing subopposite arrangement of secondaries,  $\times 7$ . Fig. 8. Detail of teeth,  $\times 6$ . Fig. 9. Overview of margin,  $\times 2.2$ . Figs. 10 & 11. Detail showing secondary, tertiary, and higher order venation and aeroles,  $\times 10$ .



Figures 12–20. Details of leaf margin and tooth morphology. Figures 12, 14–16, and 20 are of the fossil leaf, *Neviusia dunthornei*; Figures 13 and 17–19 are of the extant species, *N. cliftonii*. Fig. 12. Overview of margin,  $\times 3.2$ . Fig. 13. Leaf margin, showing crowded teeth,  $\times 10$ . Fig. 14. Detail of higher order venation,  $\times 15$ . Figs. 15 & 16. Detail of tooth from fossil leaf to show venation,  $\times 6$ ; note accessory veins; Figure 15 is a negative image to increase contrast. Figs. 17 & 18. Detail of tooth venation,  $\times 10$ ; note accessory veins. Fig. 19. Margin showing teeth and details of venation,  $\times 10$ . Fig. 20. Margin showing teeth and venation,  $\times 6$ .

Compound agrophic veins, composed of four to six tertiaries each, extend from secondaries to the margin in the basal part of the leaf at angles of 25–30° to vascularize the marginal teeth at the tips of the lobes (Figures 1, 5, at arrow). Third-order veins form moderate, convex to sinuous curving braces between adjacent secondary veins that are perpendicular to the midrib, between secondary and agrophic veins and between adjacent agrophic veins (Figures 5, 10, 20). Fourth- and fifth-order veins are regular polygonal reticulate. Aéroles are well developed and 5+ sided (Figures 10, 14, 20).

The leaf margin is serrate with two to three sizes of regular and accessory teeth (Figures 3, 12, 15, 16, 20). Regular teeth occur at around 3 mm intervals, either singly or paired and grouped with one or two accessory teeth. Regular teeth are 2 mm long, flexulous apical, flexulous basal (Figures 3, 15, 16, 20). Each regular tooth is vascularized medially by an agrophic tertiary vein, with additional smaller accessory veins entering the vein on either side (Figures 3, 12, 15, 16, 20). Accessory veins are around 1 mm long and concave apical, flexulous basal to straight apical, flexulous basal (Figures 3, 12, 16).

#### DISCUSSION

*Neviusia dunthornei* is assignable to the genus *Neviusia* on the basis of distinctive features of the leaf shape, venation, and leaf margin. Whereas the tribe Kerrieae was established on the basis of floral features, the included taxa also have leaves with distinctive morphology. The Rosaceae encompasses a wide array of leaf morphologies, including clearly simple leaves that are entire to lobed as well as leaves that are so deeply dissected as to appear palmately and pinnately compound (Wolfe and Wehr 1988). Many rosaceous leaves have a serrate margin. However, a survey of leaf types within the family shows that entire and simply-lobed leaves typically have either a single, very regular type of tooth (e.g., many *Prunus* leaves) or, if more than one size order, the teeth are of the same type (e.g., *Malus*). Leaves of the tribe Kerrieae are unusual in having entire to lobed leaves with a serrate margin with 2 to 3 size orders of teeth of differing morphologies (regular teeth are flexulous apical, flexulous basal; accessory teeth may be concave apical, flexulous basal to straight apical, flexulous basal). Other rosaceous leaves with complex tooth marginal patterns of the type seen in Kerrieae otherwise usually occur in groups typified by highly dissected laminae, such as the blackberries (*Rubus*).



The three genera that compose the tribe Kerrieae can also be distinguished from one another based on several features of leaf morphology, venation, and margin. *Kerria* leaves are narrow and ovate with a length/width ratio of 2.1–2.5:1, and often have a long, attenuated leaf apex. *Rhodotypos* leaves are generally more isodiametric with a length/width ratio around 1.1:1 and have subopposite secondary veins, in contrast to the more distinctly alternate secondaries more characteristic of *Kerria* and *Neviusia*. Tertiary veins are considerably denser in *Kerria* and *Rhodotypos* than in *Neviusia*, and also tend to be more consistently perpendicular to the secondaries, while those of *Neviusia* are more variable and can sometimes result in an inverted V (“chevron”) pattern.

Of the two extant species of *Neviusia*, the fossil is considerably more similar to *N. cliftonii* of the Mount Shasta region of northern California (Figures 2, 4, 6, 8, 9, 11). Both of these leaves are broadly ovate with secondaries that are subopposite from one another (Figures 5, 7, 8). The leaf margins in both are serrate with 2–3 orders of relatively coarse teeth with comparable shapes and venation patterns (Figures 10–20). In contrast, leaves of *N. alabamensis* are more elongate, have much finer teeth at the margin, and have secondary veins that are more pronouncedly alternate. Details of leaf margin are very similar in the fossil and *N. cliftonii*. They show similar variation in tooth size (Figures 3, 9), tooth morphology (Figures 3, 4, 8, 17–20), distribution of different morphological types (Figures 3, 6, 9, 12), and even degree of crowdedness (Figures 3, 12, 13, 18). The fossil differs from both extant species in having thicker midrib and primary veins (Figure 7).

**Phytogeographic significance.** The fossil record of the entire tribe Kerrieae is limited to this northwestern occurrence of *Neviusia* (Wehr and Hopkins 1994). Together with its modern distribution, the occurrence of *Neviusia* in the Okanogan Highlands suggests that the Kerrieae radiated from Asia into western, and subsequently southeastern North America, but never became a major North American element. It is interesting that *N. cliftonii*, the California native, has what might be considered less derived features (based on trends found in other tribes of Rosaceae) in comparison to the southeastern *N. alabamensis*. These include a loss of petals and an increase in number of stamens. This species also has a generally more elongate style as well as more lanceolate leaves than *N. cliftonii* (Shevock et al. 1992). The similarity of *N. cliftonii* and the fossil *N. dunthornei* leaves is consistent with an origin or early diversification of the genus in the Northwest, with

montane northern California serving as an early refugium, while forms that made it to the warm temperate Southeast apparently diversified further. It is notable that *Neviusia* has not been found in the extensive Eocene floras of the Mississippi Embayment, such as those of the Claiborne Formation (Dilcher 1971). The lack of Rosaceae in southeastern floras that are generally contemporaneous with Okanogan Highlands floras may be because of warmer regional conditions that at that time produced a more megathermal, possibly dry-adapted flora dominated by Lauraceae and early legumes (Graham 1999). Perhaps the arrival of *Neviusia* in southeastern North America occurred much later in conjunction with the climatic deterioration of the Neogene.

#### TAXONOMIC TREATMENT

***Neviusia dunthornei*** DeVore, Moore, Pigg & Wehr, *sp. nov.*

Family: Rosaceae

Tribe: Kerrieae

Genus: *Neviusia* A. Gray.

TYPE SPECIES: *N. alabamensis* A. Gray

SPECIES DIAGNOSIS: Leaves broadly ovate, lobed; 4.9 cm long  $\times$  5.6 cm wide; L/W ratio 0.88:1; apex acute; midrib thick; venation craspedodromous; secondary veins forming acute angle, 30° to midrib, subopposite; compound agrophic veins forming acute angles 25–30° with secondaries; tertiaries forming moderate, curving braces between adjacent secondaries, secondaries and agrophic and adjacent agrophic veins; areoles 5–6 sided with freely ending veinlets; 4th and 5th order veins regular polygonate reticulate; margins serrate, two (occasionally three) size orders of regular and accessory teeth, regular teeth occurring at 3 mm intervals, solitary or paired, grouped with one or two accessory teeth, regular teeth 2 mm long, flexulous apical flexulous basal, vascularized medially, often with two lateral accessory veins, accessory teeth 1 mm long, concave apical flexulous basal to straight apical flexulous basal.

HOLOTYPE: UWBM 54169 (Figures 1, 3, 7). Collected by *Peter Dunthorne*, 1991.

PARATYPE: UWBM 97148 (Figures 5, 11, 19). Collected by *Peter Dunthorne*, 1991.

Type locality: CANADA. British Columbia: One Mile Creek, near Princeton (UWBM B 3389; *Crane & Stockey*, 1987).

Age and Stratigraphy: Allenby Formation, Lower-Middle Eocene.

ETYMOLOGY: The specific epithet, *dunthornei*, is named in honor of Peter Dunthorne of Sedro-Woolley, Washington, for his numerous contributions to the collecting of the Okanogan Highlands floras.

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